A CONTRIBUTION TO THE LIFE HISTORY OF *APOCYNUM ANDROSAEMIFOLIUM*.

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(WITH PLATE II)

IT appears that not one of the Apocynaceae, a family of about 1000 species, has ever been studied carefully in reference to the minute morphology of the flower. Considering this in connection with the fact that the family stands near the Asclepiadaceae, with their peculiar pollen and stigma, it was believed that it deserved investigation. Buds and flowers of *Apocynum androsaemifolium* L. were collected in various stages, and the results of their investigation are herewith described.

The order of appearance of the floral whorls is centripetal. The calyx shows no peculiarities other than a ruffling of the epidermis on the abaxial surface near the base, suggesting a mechanism for the folding of the sepals.

Each petal of the campanulate corolla has on its inner surface near the base a ridge (*fig. 1, r*) running from the midrib diagonally outward and toward its base. It is highest at the midrib, and undoubtedly functions as an aid in compelling cross-pollination. The ridge arises from the more superficial cells of the leaf, and does not affect the course of the veins. Its meristematic crest forms the cells for its enlargement.

The stamens are peculiar in form, adjusting themselves neatly in a ring rather closely applied to the stigmatic head (*fig. 1, s*). At the base of each are two long auriculate appendages (*figs. 1, 2, 3, ap*) extending downwards dorsal to the filament. The sporangia are above the insertion of the filament, and do not extend into the appendages. The loculi open on their inner surfaces, somewhat laterally, by longitudinal slits, and immediately beneath them is a beard of epidermal hairs extending transversely across the faces of the anthers, forming a ring around the stigmatic head (*figs. 1, 2, b*). These hairs meet similar ones from a ring around the head, thus preventing pollen from rolling into the base of the flower.

In the development of the stamen the enlargement of the tip, foreshadowing the formation of sporogenous tissue, occurs just about the time the carpels appear. The hypodermal layer gives rise to a primary parietal layer, and another homologizing with what is ordinarily the primary sporogenous layer (*fig. 4*). The former divides once; the latter also divides, forming the tapetum and primary sporogenous cells (*fig. 5*). This has been observed in a few plants only (**1**), the tapetum usually arising from the primary parietal layer. The primary sporogenous cells elongate as they do in Asclepias (*fig. 6*), but divide into a mass of mother cells, thus reinforcing the presumption that in Ascelpias this stage is simply omitted. The pollen is in the mother cell stage when the ovules appear. The rounded mother cells do not always divide simultaneously. Division of the two daughter cells is simultaneous or nearly so (*fig. 8*), and almost so in all the daughter cells of a sporangium; but not in different stamens of the same flower. Sometimes one daughter cell fails to divide, and three microspores instead of a tetrad is the result (*fig. 9*). Occasionally some of the pollen grains near the tip of the sporangium disintegrate after tetrad division, probably serving as nourishment for the others. The whole tapetum also disintegrates soon after tetrad division.

The microspores remain in tetrads in maturity, and their arrangement with relation to each other is various. In fact, one can find all stages grading from the bilateral to the tetrahedral arrangement. *Fig. 10* evidently resulted from the spindles in the second division being somewhat at right angles in the same plane, and is like a grouping found by WILLE (**2**) in *Orchis mascula*. Usually the four spores are in the same plane, but their arrangement with regard to each other varies; in *fig. 11* four pollen grains meet at a point on each side of the group; in other cases there are four on one side and three on the other; in still others only three meet at a point on either side. The pollen grains in a tetrad are often plainly unequal in size. In such a group as is represented in *fig. 11*, suppose the upper half (cells *a* and *b*) were revolved on the lower half 90°, with *xy* as an axis; if then they adjusted their form to fit each other the result would be the prevailing dicotyl grouping—tetrahedral. *Figs. 11, 12, 13* are three members of a series grading from the bilateral to the tetra-

hedral form, varying only in degree of rotation and in mutual adjustment. Both forms may thus occur in the same plant. However, the tetrahedral form is not common; most of the groups are like *figs. 11* and *12*, similar to those found in *Typha latifolia* (**3**). A case like Zostera (**4**), with its long pollen mother cells dividing lengthwise, makes it doubtful whether pressure is much of a factor in determining the direction of the spindles. The spindles in the microspore daughter cells of *A. androsaemifolium* seem to lack definiteness in direction.

The formation of the generative and tube nuclei occurs when the ovules are in the sporogenous cell stage. The division is not simultaneous in the same sporangium, nor even in the same tetrad; the division is complete by the time the embryo sac has reached its 8-celled stage. The generative cell is lenticular or fusiform, as in Asclepias. Two spherical male cells are formed about the time the embryo sac is ready for fertilization, and while the pollen is still in the anther. STRASBURGER (**5**) observed a small and a large nucleus in the pollen of *Vinca major*, and again found both nuclei in cultures of the pollen tubes. If these were tube and generative nuclei, Vinca differs from *A. androsaemifolium* in the time of the division of the generative cell. STRASBURGER also observed (**5**) a tube nucleus and two smaller ones, probably male cells, in *Amsonia salicifolia*, which seems to indicate that this one agrees with *A. androsaemifolium* in the time of male cell formation.

At the base of each petal and alternating with the stamens are five glands resembling those in Asclepias. They originate shortly after the floral parts appear and are said to be nectariferous (**6**).

The two carpels unite at their tips before ovules are formed, and just after sporogenous tissue appears in the stamens. The tips form a rounded lump or head with glandular epidermis over large portions of it, as in the Asclepiadaceae. The ovules are arranged in the same way as in the family just mentioned, and have the same form. The archesporial cell is of hypodermal origin and does not divide to form a primary parietal cell (*figs. 15* and *16*). A single integument deeply buries the nucellus and primary sporogenous cell. The latter divides into four megaspores, any one of which may become the embyro sac. In *fig. 19* the innermost spore becomes the sac;

in *figs. 17* and *18* it is hard to tell which spore will dominate; and in other cases the spore nearest the micropyle functions. The embryo sac passes through the regular stages to the eight-celled stage. BILLINGS (**7**) figures an embryo sac of *Amsonia salicifolia* with endosperm surrounded by an absorbing layer, and states that *Apocynum androsaemifolium* has no such layer, which we confirmed. A section through the ovules of *A. androsaemifolium* can hardly be distinguished under the microscope from a similar one of Asclepias, so great is the similarity in minute detail.

The pollen rolls out of the anthers upon the head, but is prevented by the pericephalous beard from reaching the stigma which is immediately beneath it. An insect having pollen on its proboscis, reaching after nectar, must insert it between the bases of the anthers, on account of the ridges on the corolla and the basal appendages of the stamens. The proboscis in withdrawal naturally slips into the crevices between the stamens and the head. The sticky, glandular stigma holds some of the pollen, while the pericephalous beard, acting as a brush, increases the probability of pollen remaining at the stigma (*fig. 1*). The head above the beard is glandular and the pollen sticky; therefore as the proboscis is withdrawn through the hairs it picks up a load of pollen for the next flower (*fig. 1*). KUNTH (**6**) gives a short account of the manner of pollination.

The chief facts are the origin of the tapetum from the homologue of the primary sporogenous layer instead of the primary parietal layer; the gradation between bilateral and tetrahedral microspore arrangement; the absence of a primary parietal cell in the ovule; the single layer of cells composing the nucellus; and the great similarity in the internal structure of the flowers of Apocynum and Asclepias.

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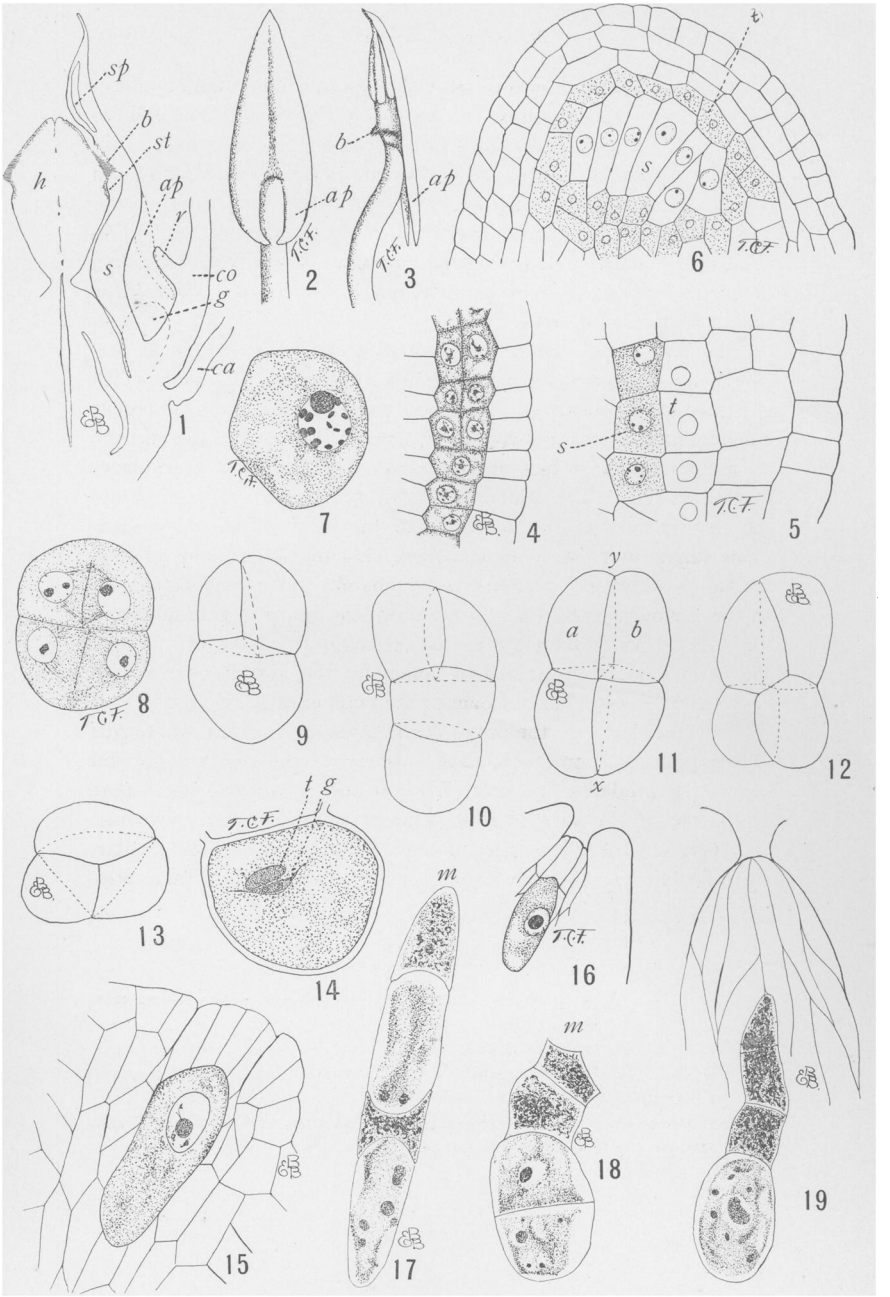

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EXPLANATION OF PLATE II.

All figures were drawn with a camera lucida unless otherwise stated, and a Leitz 1–12 oil immersion objective was used for all figures requiring high magnification. The figures have been reduced to one-half the original drawings, to which the indicated magnifications apply.

FIG. 1. Longitudinal section of the flower, semi-diagramatic: *ca*, calyx; *co*, corolla; *r*, ridge; *g*, gland; *s*, stamen; *ap*, appendage; *sp*, sporangium; *b*, beard; *h*, head; *st*, stigma.

FIG. 2. Abaxial view of stamen: *ap*, appendages; without camera lucida.

FIG. 3. Lateral view of stamen: *ap*, appendages; *h*, head; without camera lucida.

FIG. 4. Longitudinal section of anther showing origin of primary parietal layer. ×1800.

FIG. 5. Longitudinal section of anther: *s*, primary sporogenous cells; *t*, tapetum. ×2650.

FIG. 6. Cross section of anther: *t*, tapetum; *s*, primary sporogenous cells. ×1110.

FIG. 7. Microspore mother cell before tetrad division. ×3300.

FIG. 8. Microspore daughter cells in simultaneous division. ×3300.

FIG. 9. Three pollen grains from a mother cell. ×2250.

FIGS. 10–13. Various arrangement of pollen grains in tetrads. ×2250.

FIG. 14. Pollen grain: *t*, tube nucleus; *g*, generative cell. ×2650.

FIG. 15. Section of ovule showing archesporial cell enlarged and functioning as primary sporogenous cell; single integument; nucellus one layer of cells. ×2270.

FIG. 16. Same as *fig. 15;* integument closing. ×1400.

FIG. 17. Four megaspores; first and third disintegrating; *m*, micropylar end. ×3300.

FIG. 18. Four megaspores; first two disintegrating; *m*, micropylar end. ×3300.

FIG. 19. Four megaspores and nucellus; first three disintegrating. ×3300.